WOODY INVASIVE SPECIES AND THEIR ROLE IN ALTERING FIRE REGIMES OF THE NORTHEAST AND MID-ATLANTIC STATES

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ABSTRACT

Invasive plants are increasingly recognized as serious threats to biodiversity and native ecosystems in the eastern United States. This is especially true for early successional habitats, which support many of the rarest bird, insect, and plant species in the region. These habitats have historically been maintained, in part, by fire; shrub invasion can alter their fire regimes and degrade ecosystem functions. Overall flammability may be increased or decreased depending on original conditions and the inherent flammability of the invading species. Management activities (e.g., cutting) may increase flammability where the invading species left untreated depresses it. Use of prescribed fire to control invasive species is often counter-productive because burns are typically conducted during the dormant season. A short-term reduction in plant cover is usually followed by rapid increases in stem density as invasive and non-invasive plants resprout. Additional research is needed to determine how to control both native and nonnative invasive woody species, especially in early successional habitats. In this paper we review what is known about the ecology of some of the most common invasive woody species in the Northeast and discuss the physiological basis for timing control efforts to coincide with the phenology of carbon allocation, depletion, and recovery in woody plants. We review current management strategies and identify research needs for developing new strategies for invasive species control.

keywords: carbohydrate reserves, fire, invasive species, Mid-Atlantic, Northeast.

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INTRODUCTION

Woody species, both native and nonnative, are increasingly invading upland habitats in the northeastern United States. Natural disturbances such as fire, wind, and ice storms, as well as insect and disease outbreaks, facilitate the invasion of wooded tracts by invasive species that impact native vegetation. Especially susceptible to invasion are lands formerly kept open by cultivation and grazing, or used for intensive timber production. The invasion by woody species into these lands is of particular concern because they are important as wildlife habitat and for aesthetic purposes in a region that is primarily wooded. Invasive species compete with native species directly, alter ecosystem processes, may change hydrological characteristics of an area, and, in the case of nonnative species, may hybridize with native species and thereby degrade gene pools (Randall 1996). Examples of woody invaders include oriental bittersweet (*Celastrus orbiculata*), a vine that climbs up trees and eventually strangles them (Weatherbee 1994); Japanese barberry (*Berberis thunbergii*), which has been associated with adverse changes in soil pH (Kourtev et al. 1998); glossy buckthorn (*Frangula alnus*), which invades rapidly and crowds out a diverse assemblage of native species (Randall and Marinelli 1996); and gray dogwood (*Cornus racemosa*), a native shrub, which invades old fields and grasslands, changing habitat structure and composition for grassland birds including grasshopper sparrows (*Ammodramus savannarum*), bobolinks (*Dolichonyx oryzivorus*), and harriers (*Circus cyaneus*) (Mitchell 2000). Invasive species may alter fire regimes by decreasing the amount or flammability of grass fuels or by increasing the potential for high intensity fires when control efforts increase loadings of dead, downed woody material.

In the Northeast and Mid-Atlantic states, early successional ecosystems (grasslands, heathlands, and abandoned farmlands) provide important habitats for many regionally rare species including grassland birds, butterflies and moths, and several plant species. Historically open lands have been important as habitat for game species, for their aesthetic value, and for increasing habitat diversity regionally. Fields were kept open by mowing and grazing beginning in Colonial times. Before that, Native Americans burned fields to keep them open (Olson 1978, Stevens 1996), and this practice was continued into the 20th century by European settlers. Shifts in agriculture to the Midwest, increased effectiveness of fire suppression efforts, and increased concern over the effects of open burning on air quality have reduced the influence of fire in these ecosystems, resulting in increased opportunities for woody species to invade grasslands and old fields.

On many sites, native forests have replaced open land, but on other sites, shrubs and vines originally planted as hedgerows or ''wildlife plantings'' have invaded abandoned fields. Exotic species, including multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*), and Asian honeysuckles (*Lonicera* spp.), produce prolific amounts of seed allowing them to spread quickly without natural diseases or insect pests to keep them in check. Many invasive plants also reproduce vegetatively and may actually thrive when open lands are mowed or burned to keep them in check. Although ineffective in many instances, dormant-season mowing and burning are still recommended for reducing shrub cover in grasslands (Jones and Vickery 1997). Burning during the dormant season is consistent with traditional Colonial practices (when it was often combined with grazing and hence more effective), but the danger of escaped fires is greater than when burns are conducted during the growing season when the moisture content of vegetation is high. Mowing is an alternative to burning, but mechanical treatments require large capital investments for machinery and may result in a dense thatch that is unsuitable for grassland bird use. Herbicides are effective when applied in conjunction with mechanical treatments and/or when applied to individual plants, but are expensive, inappropriate, or inefficient for use in some situations (e.g., in watersheds protecting drinking water supplies and in natural areas supporting rare plant species that might be adversely impacted by broadcast sprays). Both mechanical treatments and herbicide applications can alter fuel bed characteristics to increase the intensity of wildfires burning through treated vegetation.

Additional research is needed to determine how to control both native and nonnative invasive woody species, especially in early successional habitats. In this paper we review what is known about invasive species ecology in the Northeast and discuss the physiological basis for timing control efforts to coincide with the phenology of carbon allocation, depletion, and recovery in woody plants. We review current treatment practices and identify research needed to develop new strategies for invasive species control.

SPECIES OF CONCERN

Invasive shrubs and small trees, both native and nonnative, are common throughout the Northeast and Mid-Atlantic states and are spreading from disturbed areas into natural areas (Randall and Marinelli 1996). Asian honeysuckles, Japanese barberry, autumn olive, winged euonymus (*Euonymus alata*), multiflora rose, gray dogwood, black locust (*Robinia pseudoacacia*), and European (*Rhamnus cathartica*) and glossy buckthorn all form dense thickets that effectively out-compete native shrubs and herbaceous species and severely alter structure of open habitats. Native species, especially if planted beyond their pre-Columbian ranges, may be similarly aggressive. Examples include gray dogwood, black locust, and false indigo (*Amorpha fruticosa*). Restoring open conditions often requires removing or dramatically reducing the density of invasive species. Successful management requires knowledge of individual species' growth habits and ecological requirements. Here we summarize what is known about some of the species that are among the most aggressive invaders in the Northeast and Mid-Atlantic states. (See Table 1 for additional species and information.)

Japanese Barberry

Japanese barberry (*Berberis thunbergii*) is a dense, rounded spiny shrub that is usually broader than tall at maturity. Individuals may grow to almost 3 m tall, although 1–2 m is more common, with widths of 1–2.5 m (Dirr 1990, Gleason and Cronquist 1991). It is one of the first shrubs to leaf out during the spring and flowers during April–May. Native to Japan, it was introduced to the United States during 1864 as an ornamental and Dirr (1990) currently lists 29 cultivars. It has invaded pastures, woodlands, ledges, and floodplains (Weatherbee et al. 1998), in part because the fruits are dispersed by birds. Barberry has been controlled by hand-pulling or digging, herbicide application to sprouts after cutting, and prescribed fire (Randall and Marinelli 1996).

Russian and Autumn Olive

Russian and autumn olive (*Elaeagnus angustifolia* and *E. umbellata*) are tall (4–5 m) spreading shrubs or small trees. They flower during May–June and their seeds are dispersed by birds. Russian olive is native to southern Europe and Asia and has long been cultivated in Europe. Autumn olive is native to mountain streambank and thicket habitats in China, Korea, and Japan and was introduced to the United States around 1830 (Dirr 1990, Randall and Marinelli 1996). In the past, the U.S. Soil Conservation Service planted these species to stabilize soils, especially along roadsides as both species are highly salt tolerant and can fix atmospheric nitrogen (Dirr 1990). They were also used as a natural screening and for wildlife plantings (Weatherbee et al. 1998) and are dispersed by birds and mammals. Russian olive is more common in the central and western U.S., whereas autumn olive is common throughout the northeastern, mid-Atlantic, and northern midwestern states (Gleason and Cronquist 1991). These shrubs are most common in abandoned fields and grasslands where they grow quickly

Table 1. Management-related aspects of nineteen invasive woody species in the Northeast and Mid-Atlantic states.

Species	Native or exotic	Range of problem	Reproduction and dispersal	Impacts on native habitats	Control methods	Reference[a]
Trees						
Acer platanoides L. Norway maple	Exotic, from Eurasia	MA and s. ON to Washington, D.C. Range may be larger as it is easily mistaken for sugar maple	Seeds and stump sprouts. Wind dispersed	Loss of herbaceous species diversity under trees. Out-competes native sugar maples and beeches in mesophytic forests	Hand pull. Cut mature trees close to the ground	Randall and Marinelli 1996
Ailanthus altissima Tree-of-heaven	Exotic, from China	MA and s. ON to TX and FL	Many wind blown seeds. Root and stump sprouts	Displaces native vegetation. Forms large clonal stands	Repeated and persistent cutting. Cutting followed with herbicide application to the stump	Randall and Marinelli 1996, Clark et al. 1998
Robinia pseudoacacia Black locust	Native to PA and IN, south to GA and LA	Introduced and naturalized north and west of its native range	Seeds and root sprouts. Wind dispersed	Displaces native vegetation. Forms large clonal stands	Repeated and persistent cutting. Cutting followed with herbicide application to the stump	Randall and Marinelli 1996, Weatherbee et al. 1998
Shrubs						
Amorpha fruticosa False indigo	Native to PA and OH to MN to FL	Introduced and naturalized in the eastern and middle states.	Likely by seeds and sprouts	Displaces native vegetation	Not known	Gleason and Cronquist, 1991
Berberis thunbergii Japanese barberry	Exotic, from Asia	Throughout the eastern and midwestern U.S.	Seeds and stump sprouts	Invades old fields and early successional woodlands. Shades out native understory species. Common in some pine plantations	Hand pull or dig smaller shrubs. Cutting followed with herbicide application to the stump in cases of larger individuals. In Midwest, fire has reduced some populations	Randall and Marinelli 1996, Ehrenfeld 1997, Silander and Klepeis 1999
Cornus racemosa Gray dogwood	Native, ME and s. ON to VA to MN	Upstate NY. Other areas unknown	Seeds and sprouts from rhizomes. Bird and mammal dispersed	Invades old fields and pastures. Forms dense clones that degrade grassland bird habitat and displaces native herbaceous vegetation	Repeated mowing can keep some areas open. Regular growing season cutting or burning may be most effective at reducing density	Mitchell 2000
Cytisus scoparius Scotch broom	Exotic, from Europe	Nova Scotia, NY to GA with several populations in New England, Pacific Northwest to central CA	Prolific long-lived seeds. Sprouts from the root crown	Forms large thickets that displace native vegetation. Its flammability brings fire to the tree canopy. It invades rapidly after logging, clearing or burning	Pull or dig out plants for small patches. Basal bark herbicide application. Prescribed fire followed by hand pulling seedlings from the seedbank	Hoshovsky 1986, Randall and Marinelli 1996
Elaeagnus umbellata Autumn olive	Exotic, from Asia	Midwestern, northeastern, and southeastern U.S.	Prolific seeds. Seeds are bird dispersed. It also sprouts when cut	Forms large thickets that displace native vegetation	Pull or dig out plants. Multiple herbicide applications have been successful. Periodic fires or cutting do not control this species	Randall and Marinelli 1996, Clark et al. 1998

Table 1. Continued.

Species	Native or exotic	Range of problem	Reproduction and dispersal	Impacts on native habitats	Control methods	Reference[a]
Euonymus alata Burning bush	Exotic, from Asia	Eastern U.S.	Copious seeds (bird dispersed)	Displaces native vegetation in open woods, second growth forests and pastures	Cutting followed with herbicide application to the stump. Young plants can be hand pulled	Randall and Marinelli 1996, Clark et al. 1998, Weatherbee et al. 1998
Ligustrum vulgare Common privet	Exotic, from Europe	Eastern U.S.	Seeds (bird dispersed) and suckers	Displaces native vegetation by forming dense thickets	Hand pull or dig smaller shrubs. Herbicides are also effective as a foliar application or cutting followed with application to the stump	Randall and Marinelli 1996
Lonicera maackii Amur honeysuckle	Exotic, from Asia	At least 24 eastern states plus ON	Seeds (bird dispersed). Sprouting	Displaces native vegetation by forming dense thickets. Reduces native tree regeneration by shading seedlings	Hand pull or dig smaller shrubs. Cutting followed with herbicide application to the stump in cases of larger individuals. Shrubs will resprout after burning or cutting	Randall and Marinelli 1996, Hutchinson and Vankat 1997, Deering and Vankat 1999
Lonicera morrowii Morrow honeysuckle	Exotic, from Japan	WY to ME and s. Canada	See above	See above	See above	Randall and Marinelli 1996
Lonicera tatarica Tatarian honeysuckle	Exotic, from Turkey and Russia	UT and CA to ME and s. Canada	See above	See above	See above	Woods 1993, Randall and Marinelli 1996
Rhamnus cathartica Common buckthorn	Exotic, from Eurasia	Northeastern and north central U.S.	Seeds and sprouts	Displaces native vegetation by forming dense thickets. It is an alternate host for the fungus that causes oat rust	Hand pull or dig smaller shrubs. Cutting followed with herbicide application to the stump	Randall and Marinelli 1996
Frangula alnus Glossy buckthorn	Exotic, from Eurasia	Northeastern U.S.	Prolific seeds dispersed by birds. Root sprouts	Displaces native vegetation in wetlands and uplands	Herbicides are effective: both foliar application or cutting followed with application to the stump. Burning kills seedlings but only top-kills mature plants. Follow up herbicide treatment is necessary	Randall and Marinelli 1996, Weatherbee et al. 1998
Rosa multiflora Multiflora rose	Exotic, from Asia	ME to MN to AL	Prolific seeds dispersed by birds	It invades open lands and forms dense thorny stands	Regular mowing of open areas will prevent seedlings from becoming established. Hand pull or dig smaller shrubs. For larger shrubs cut and apply herbicide to the stump	Randall and Marinelli 1996

Table 1. Continued.

Species	Native or exotic	Range of problem	Reproduction and dispersal	Impacts on native habitats	Control methods	Reference[a]
Vines						
Celastrus orbiculata Oriental bittersweet	Exotic, from Asia	ME to GA to MN	Seeds dispersed by birds. Root suckers	Displaces native vegetation by shading it. It twines around trees eventually strangling them and making them top heavy and susceptible to wind and storm damage	Regular mowing where possible. Both foliar and cut stump herbicide applications have been successful	Randall and Marinelli 1996
Lonicera japonica Japanese honeysuckle	Exotic, from Asia	MA to IL and MO to TX and FL	Seeds dispersed by birds	Displaces native vegetation by shading it. It climbs over the tops of shrubs and small trees eventually smothering them and will climb to the canopy in gaps	Foliar herbicide application is often required. Pulling, cutting or burning stimulates new growth	Randall and Marinelli 1996
Smilax rotundifolia Catbrier	Native, Nova Scotia to MN, south to FL and TX		Rhizomes and seeds	It can climb over the tops of shrubs and small trees, shading them. It is flammable and acts as a ladder fuel	Smilax is resistant to herbicides. Rhizomes can persist for years after above-ground stems are removed	Gleason and Cronquist 1991, Carey 1994

[a] Additional information on invasive species is available from The Nature Conservancy, Wildland Invasive Species Program (http://tncweeds.ucdavis.edu/), the U.S. Forest Service Fire Effects Information System (http://www.fs.fed.us/database/feis/), and state weed control and/or wildlife agencies.

and form dense thickets. Control efforts have included cutting trees followed by herbicide application to the stumps and pulling small plants (Randall and Marinelli 1996, Clark et al. 1998).

Asian Honeysuckles

Introduced Asian honeysuckles (*Lonicera* spp.) are multi-stemmed shrubs that can grow tall and tree-like or shorter and densely branched, or as vines depending on species and habitat. Many species of honeysuckle and their nearly 180 cultivars occur in the United States, including several native species. The most problematic nonnative species (*Lonicera maackii*, *L. morrowii*, *L. tatarica*, *L. xylosteum*, *L.* × *bella*) are shrubs 2–4 m tall whose dense thickets shade out ferns, grasses, and wildflowers (Clark et al. 1998). In North America these species are easy to culture and propagate, and are generally not susceptible to damaging insects and diseases, which makes them well suited for landscaping. Unfortunately, these same characteristics also make them noxious weeds that invade natural areas in profusion. Honeysuckles produce large quantities of berries, which are eaten by birds, resulting in the spread of seeds into un-invaded areas, particularly young forests and floodplains (Weatherbee et al. 1998). Unlike other honeysuckle species, Japanese honeysuckle (*Lonicera japonica*) is a vine that has similarly become a noxious weed in the U.S. It invades successional forests and edge habitats and chokes supporting trees and shrubs by twining tightly around them (Weatherbee et al. 1998). Many of the honeysuckles were introduced during the late 1700s and 1800s and include several varieties and forms. Like several of the invasive species already mentioned, the bush honeysuckles were promoted by the U.S. Soil Conservation Service for erosion control and wildlife cover (Clark et al. 1998). Hand pulling and cutting followed by herbicide application to the stumps have been successful methods to manage some honeysuckle populations (Randall and Marinelli 1996).

Glossy and Common Buckthorn

Glossy buckthorn, also known as alder buckthorn (*Frangula alnus*), is a large shrub or low branched tree 3–5 m tall. Common buckthorn (*Rhamnus cathartica*) is a larger tree of 6–8 m tall. Both species are native to Europe and Asia and have become naturalized in the eastern U.S. since their introduction as hedges and wildlife habitat prior to 1800 (Clark and Mattrick 1998). While common buckthorn prefers upland sites and glossy buckthorn prefers wetland sites, both species can grow in wet or dry habitats and are tolerant of dense shade. Both species flower and fruit throughout the growing season (Weatherbee et al. 1998). They are often overlooked as they do not possess showy flowers or fruits, although they are easily observed during the early spring and late fall as they leaf out earlier and hold their leaves longer than native species. This longer growing season may give them a competitive advantage over native species (Clark and Mattrick 1998). Although their cathartic fruits are somewhat poisonous to birds and wildlife, they are nevertheless eaten by birds which disperse them across the landscape. Control efforts have included hand-pulling smaller plants and cutting followed by herbicide application to stumps. Stems resprout after cutting (in some cases even after herbicide application). Little is known regarding the longevity of seeds in the soil.

Multiflora Rose

Multiflora rose (*Rosa multiflora*) has a growth form similar to a fountain with long, slender, recurving branches (Dirr 1990). It can grow 1–3 m high with a spread of 3–5 m. It has an exceptionally high growth rate: stems can elongate 0.6 m or more per year. Multiflora rose is native to Japan and Korea and escaped from cultivation in the U.S. following its introduction during 1868. It was originally promoted by the U.S. Department of Agriculture as a living fence and was distributed to farmers for this purpose (Weatherbee 1994). Birds, which eat its abundant fruits, disperse this species into roadsides, pastures, open woods, and undisturbed areas. Due to its thorny branches, multiflora rose is not browsed and therefore spreads rapidly once established. Control using repeated cutting and herbicide application has been successful in some areas (Randall and Marinelli 1996).

Tree-of-heaven

Tree-of-heaven (*Ailanthus altissima*) is a fast growing (1–2 m/year), pollution tolerant, deciduous tree of 10–20 m in height. It is native to China, but has naturalized over much of the U.S. after being introduced during 1784 (Dirr 1990). It spreads by both seeds and root suckers and is resistant to disease and pests (Clark et al. 1998). Although often observed in abandoned fields or open meadows and within cities, it has also been observed growing in gaps in the forest (both natural and resulting from logging; Clark et al. 1998, Knapp and Canham 2000). Successful control efforts include persistent cutting (multiple years, multiple cuts per year) and cutting followed by herbicide application (Randall and Marinelli 1996).

Gray, Red Osier, and Silky Dogwoods

Gray, red osier, and silky dogwoods (*Cornus racemosa*, *C. sericea*, and *C. amomum*, respectively) are medium-sized shrubs (1–5 m tall) that often form dense thickets (Gleason and Cronquist 1991). They occur in moist-to-wet habitats and, although native to the Northeast, have become invasive in old-field habitats of New York state. To maintain old fields as grassland bird habitat, it is necessary to prevent dogwood species from dominating these sites. Prescribed fire and mowing activities during the dormant season have had limited success in controlling dogwood invasion, although recent attempts using growing season treatments have had some success (Mitchell 2000).

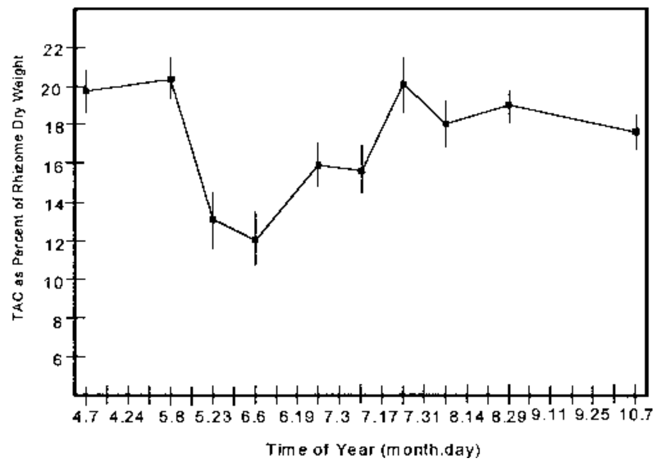

Fig. 1. Seasonal fluctuation in total available carbohydrates (TAC) in huckleberry (*Gaylussacia baccata*) rhizomes, average of 3 plots. Error bars are 95% confidence limits. From Droege 1996.

Black Locust

Black locust (*Robinia pseudoacacia*) is a deciduous tree with furrowed bark that grows to 25 m tall. It is native to the United States south of Pennsylvania and southern Indiana. Because of its nitrogen-fixing capabilities and its hard, high quality wood, it has been widely planted and has become naturalized throughout most of the United States and southern Canada, as well as parts of Europe and Asia (Randall and Marinelli 1996, Hardin et al. 2001). Black locust generally occurs in early successional habitats following disturbance (Clark et al. 1998). It vigorously root suckers as well as sprouts from the stump, often producing large spreading colonies connected by a single root system (Clark et al. 1998). Cutting followed by immediate application of herbicide to the stump has been successful in killing this species (Randall and Marinelli 1996, Weatherbee et al. 1998).

PHYSIOLOGICAL BASIS FOR MANAGEMENT

Carbohydrate reserves in roots and shoots of plant species provide an energy source to support growth and respiration prior to leaf-out (and subsequent production of photosynthate) as well as after disturbance such as herbivory or fire (Cook 1966, Loescher et al. 1990, Kozlowski 1992, Rodgers et al. 1995, Sakai et al. 1997). These reserves vary seasonally (Donart 1969, Kramer and Kozlowski 1979, Loescher et al. 1990, Johansson 1993, Droege 1996): reserves are depleted during budbreak and subsequent growth in the spring, replenished during the growing season, and gradually used in respiration during the dormant season (Figure 1). This cycle of storage and utilization is evident in woody and herbaceous perennial species (Cook 1966, Coyne and Cook 1970, Westhafer et al. 1982, Zasada et al. 1994). Management actions can have differing, long-term effects depending on when they are applied relative to this cycle (Loescher et al. 1990, Kays and Canham 1991).

Early studies of carbohydrate reserves focused on range and horticultural species (Cook 1966, McConnell and Garrison 1966, Donart 1969, Priestley 1970). Cook (1966) reported that stem elongation and rate of growth during the spring is proportional to the amount of carbohydrate reserves for woody plants. McConnell and Garrison (1966), in their study of bitterbrush (*Purshia tridentata*), state that herbage removal is least detrimental to shrub vigor when done during the winter dormant season. More recent studies have reported on the positive relationship of carbohydrate reserves to growth, establishment, and vigor of trees (Abod and Webster 1991, Johansson 1993, Zasada et al. 1994). Bowen and Pate (1993) report that fire-resistant sprouters have disproportionately large roots containing high concentrations of carbohydrates and nutrients compared to species that do not sprout. Species that sprout also have lower growth rates indicating that the storage of resources may be at the expense of growth rate (Bowen and Pate 1993, Sakai et al. 1997). Research on the effects of frequency, timing, and extent of defoliation on reserves of trees and shrubs indicate that multiple treatments, mid- to late growing season treatments, and extensive defoliation result in low autumn carbohydrate reserves (FitzGerald and Hoddinott 1983, Gregory and Wargo 1986, Kays and Canham 1991, Renaud and Mauffette 1991, Erdmann et al. 1993). Bowen and Pate (1993) found that after burning the Australian shrub *Stirlingia latifolia*, starch reserves were nearly depleted within a few months after the beginning of regrowth and were not replenished until flowering commenced during the second growing season after burning.

In woody plants, the extent of carbohydrate reserves contributes to the vigor of individual stems. With more reserves, individuals are better able to survive stress; depleted reserves often result in death (Gregory and Wargo 1986, Kozlowski 1992). Johansson (1993) reported that low numbers of sprouts or suckers after cutting or defoliation indicate low starch levels in the roots of European aspen (*Populus tremula*). Late-season defoliation can cause a decrease in carbohydrate reserves, which can impact the vigor of the individual at the beginning of the following growing season (Gregory and Wargo 1986, Loescher et al. 1990). Kays and Canham (1991) found that for red maple (*Acer rubrum*), gray birch (*Betula populifolia*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*), there was a well-defined period during the growing season when cutting resulted in low autumn starch reserves and low sprout growth rates the next year. Cutting during the dormant season did not seem to affect the spring sprouting and growth rates or the autumn root-starch levels.

The majority of research done on starch reserves of woody species has focused on tree species, particularly broadleaf trees, and the impact of cutting treatments on the amount of starch stored in roots and stems (Wargo 1979, FitzGerald and Hoddinott 1983, Gregory and Wargo 1986, Renaud and Mauffette 1991, Johansson 1993). In a study of sugar maple (*Acer saccharum*), Wargo (1979) describes the annual cycle of starch depletion and replenishment in roots along with the pattern of radial root growth. Johansson (1993) similarly reports on the annual cycle for European aspen and pubescent birch (*Betula pubescens*). FitzGerald and Hoddinott (1983) and Gregory and Wargo (1986) studied quaking aspen (*Populus tremuloides*) and sugar maple, respectively, and reported changes in the annual starch cycle due to partial or complete top removal. Both studies found a decrease in autumn starch storage with mid- to late growing season defoliation primarily due to utilization of reserves for resprouting and inadequate time for these resprouts to replenish reserves before the end of the growing season. Shrubs have annual cycles of starch storage and depletion similar to those of tree species (McConnell and Garrison 1966: bitterbrush; Bowen and Pate 1993: *Stirlingia latifolia*; Zasada et al. 1994: salmonberry [*Rubus spectabalis*]; Droege 1996: black huckleberry [*Gaylussacia baccata*]). Knowledge of the patterns and timing of starch storage and depletion of invasive woody species can assure that the timing of management practices will be most effective in achieving desired objectives.

RESEARCH NEEDS

Although some research into the causes, consequences, and management of woody plant invasions has been undertaken, knowledge of the extent of invasions in the Northeast and Mid-Atlantic states is not well documented. Further, we do not know how best to manage lands to prevent and eradicate invasive species. The effects are poorly known regarding interactions between invasive species and fire behavior and occurrence. The effects of fire on controlling or spreading invasive species are not well studied for habitats in the region. Priorities for research include: assessments of which pest plants are expanding most rapidly and into which habitats; the extent of the problem throughout the region; which habitats are most threatened with invasion; how fuels are altered by invasions; and how to eradicate or manage invasions. Timing of management actions (such as mowing or burning) appears to be crucial for controlling woody invasive species.

LITERATURE CITED

Abod, S.A., and A.D. Webster. 1991. Carbohydrates and their effects on growth and establishment of *Tilia* and *Betula*: 1. Seasonal changes in soluble and insoluble carbohydrates. Journal of Horticultural Science 66:235–246.

Bowen, B.J., and J.S. Pate. 1993. The significance of root starch in post-fire recovery of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). Annals of Botany 72:7–16.

Carey, J.H. 1994. *Smilax rotundifolia*. *In* W.C. Fischer (compiler). Fire effects information system [online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula, MT. http://www.fs.fed.us/database/feis/

Clark, F.H., and C. Mattrick. 1998. Lifestyles of invasion: three case studies. New England Wild Flower 2:13–18.

Clark, F.H., C. Mattrick, and S. Shonbrun. 1998. Rogues gallery: New England's notable invasives. New England Wild Flower 2:19–26.

Cook, C.W. 1966. Carbohydrate reserves in plants. Utah Agricultural Experiment Station Bulletin, Utah Resources Series 31:47.

Coyne, P.I., and C.W. Cook. 1970. Seasonal carbohydrate reserve cycles in eight desert range species. Journal of Range Management 23:438–444.

Deering, R.H., and J.L. Vankat. 1999. Forest colonization and developmental growth of the invasive shrub *Lonicera maackii.* American Midland Naturalist 141:43–50.

Dirr, M.A. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. Fourth edition. Stipes, Champaign, IL.

Donart, G.B. 1969. Carbohydrate reserves of six mountain range plants as related to growth. Journal of Range Management 22:411–415.

Droege, M. 1996. The seasonal variation in total available carbohydrates in rhizomes of huckleberry (*Gaylussacia baccata*) and its implications for fire management. M.S. Thesis, University of Massachusetts, Amherst.

Ehrenfeld, J.G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC.). Journal of the Torrey Botanical Society 124:210–215.

Erdmann, T.K., P.K.R. Nair, and B.T. Kang. 1993. Effects of cutting frequency and cutting height on reserve carbohydrates in *Gliricidia sepium* (Jacq.) Walp. Forest Ecology and Management 57:45–60.

FitzGerald, R.D., and J. Hoddinott. 1983. The utilization of carbohydrates in aspen roots following partial or complete top removal. Canadian Journal of Forest Research 13:685–689.

Gleason, H.A., and A. Cronquist. 1991. Manual of vascular plants of Northeastern United States and adjacent Canada. New York Botanical Garden, Bronx.

Gregory, R.A., and P.M. Wargo. 1986. Timing of defoliation and its effect on bud development, starch reserves, and sap sugar concentration in sugar maple. Canadian Journal of Forest Research 16:10–17.

Hardin, J.W., D.J. Leopold, and F.M. White. 2001. Harlow and Harrar's textbook of dendrology. Ninth edition. McGraw-Hill, New York, NY.

Hoshovsky, M. 1986. Element stewardship abstract for *Cytisus scoparius* and *Genista monspessulanus:* Scotch Broom, French Broom. The Nature Conservancy, Arlington, VA. http://tncweeds.ucdavis.edu/esadocs.html

Hutchinson, T.F., and J.L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conservation Biology 11:1117–1124.

Johansson, T. 1993. Seasonal changes in contents of root starch and soluble carbohydrates in 4–6-year-old *Betula pubescens* and *Populus tremula.* Scandinavian Journal of Forest Research 8:94–106.

Jones, A.L., and P.D. Vickery. 1997. Conserving grassland birds: managing small grasslands, including conservation lands, corporate headquarters, recreation fields, and small landfills for grassland birds; managing agricultural lands including hayfields, crop fields, and pastures for grassland birds; managing large grasslands including conservation lands, airports, and landfills over 75 acres for grassland birds. Massachusetts Audubon Society, Lincoln.

Kays, J.S., and C.D. Canham. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. Forest Science 37:524–539.

Knapp, L.B., and C.D. Canham. 2000. Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. Journal of the Torrey Botanical Society 127:307–315.

Kourtev, P.S., J.G. Ehrenfeld, and W.Z. Huang. 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. Water, Air, and Soil Pollution 105:493–501.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. Botanical Review 58:107–222.

Kramer, P.J., and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York, NY.

Loescher, W.H., T. McCamant, and J.D. Keller. 1990. Carbohydrate reserves, translocation, and storage in woody plant roots. HortScience 25:274–281.

McConnell, B.R., and G.A. Garrison. 1966. Seasonal variations of available carbohydrates in bitterbrush. Journal of Wildlife Management 30:168–172.

Mitchell, L.R. 2000. Use of prescribed fire for management of old fields in the northeast. M.S. Thesis, Cornell University, Ithaca, NY.

Olson, D.P. 1978. Southern New England forests: their past and present capacity for subsistence living. Forest Notes (Society for the Protection of NH Forests) 131:2–5, 21.

Priestley, C.A. 1970. Carbohydrate storage and utilization. Pages 113–127 *in* L.C. Luckwill and C.V. Cutting (eds.). Physiology of tree crops. Academic Press, London, United Kingdom.

Randall, J. 1996. Weed control for the preservation of biological diversity. Weed Technology 10:370–383.

Randall, J.M., and J. Marinelli. 1996. Invasive plants: weeds of the global garden. Brooklyn Botanic Garden, Brooklyn, NY.

Renaud, J.-P., and Y. Mauffette. 1991. The relationships of crown dieback with carbohydrate content and growth of sugar maple (*Acer saccharum*). Canadian Journal of Forest Research 21:1111–1118.

Rodgers, H.L., M.P. Brakke, and J.J. Ewel. 1995. Shoot damage effects on starch reserves of *Cedrela odorata.* Biotropica 27:71–77.

Sakai, A., S. Sakai, and F. Akiyama. 1997. Do sprouting tree species on erosion-prone sites carry large reserves of resources? Annals of Botany 79:625–630.

Silander, J.A., and D.M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biological Invasions 1:189–201.

Stevens, A. 1996. The paleoecology of coastal sandplain grasslands on Martha's Vineyard, Massachusetts. Ph.D. Dissertation, University of Massachusetts, Amherst.

Wargo, P.M. 1979. Starch storage and radial growth in woody roots of sugar maple. Canadian Journal of Forest Research 9:49–56.

Weatherbee, P.B. 1994. The most un-wanted plants. Massachusetts Wildlife (Spring):27–33.

Weatherbee, P.B., P. Somers, and T. Simmons. 1998. A guide to invasive plants in Massachusetts. Massachusetts Division of Fisheries and Wildlife, Westborough.

Westhafer, M.A., J.T. Law, Jr., and D.T. Duff. 1982. Carbohydrate quantification and relationships with N nutrition in cool-season turfgrasses. Agronomy Journal 74:270–274.

Woods, K.D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. American Midland Naturalist 130:62–74.

Zasada, J.C., J.C. Tappeiner, III, B.D. Maxwell, and M.A. Radwan. 1994. Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. Canadian Journal of Forest Research 24:272–277.